Developmental Times and Life Tables for Shore Flies, *Scatella tenuicosta* (Diptera: Ephydridae), at Three Temperatures

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ABSTRACT Development times and survivorship of immature shore flies and longevity and reproduction of adult shore flies, *Scatella tenuicosta* Collin, reared on algae-infested filter paper, were studied at three temperatures (constant 20, 26, and 28.5°C) through life table analysis. The development time for each individual life stage and the total time from egg to adult decreased with increasing temperature. Duration of the third (ultimate) larval instar ranged from 3.3 ± 0.09 d at 20°C to 1.4 ± 0.04 d at 28.5°C and was 1.7–1.9 times longer than the approximately equal first and second instars. Development of male and female shore flies from egg to adult needed an average of 14.5 ± 0.13, 8.2 ± 0.05, and 7.0 ± 0.04 d at 20, 26, and 28.5°C, respectively, and needed an estimated 154.4 ± 1.2 thermal units (degree days). At these respective temperatures, adult females lived 21.8 ± 2.2, 19.9 ± 2.4, and 15.0 ± 1.4 d and produced 379 ± 62, 710 ± 119, and 477 ± 83 eggs during oviposition periods of 14.3 ± 2.1, 15.0 ± 2.2, and 10.8 ± 1.4 d; daily lifetime egg production averaged 16.3 ± 2.3, 33.5 ± 3.8, and 29.7 ± 3.5. Developmental stage-specific mortality was relatively low for all life stages at all temperatures, with maximum percent mortalities of 5.7% occurring in both the egg stage and in the third instar. The highest net reproductive rate (R_o) was obtained for insects reared at 26°C and was 329.6. The intrinsic rate of natural increase (r_m) was highest at 28.5°C and was 0.430. Generation time and doubling time of the population were shortest at 28.5°C and were 12.4 and 1.6 d, respectively. Results suggested that 26°C was near optimum for reproduction.

KEY WORDS *Scatella tenuicosta*, temperature, development, fecundity, life tables

Shore flies, *Scatella tenuicosta* Collin, are principally nuisance pests in greenhouse systems, bothering greenhouse workers by their sheer numbers (Vänninen, 2001), and occasionally being of economic importance by depositing fecal specks on ornamental plants and vegetables, which can lower their esthetic appeal and thus their market value (Jacobson et al. 1999). Additionally, shore flies have been implicated in the transmission of plant pathogens (Goldberg and Stanghellini 1990, Corbaz and Fischer 1994). Typically shore flies become problematic in greenhouse environments that are heavily irrigated or use hydroponic production. These wet environments favor the growth of various species of algae, the primary food source of both immature and adult shore flies (Foote 1995).

Temperature is one important environmental condition that influences insect development rates, mortality, and birth rates (Campbell et al. 1974, Taylor 1981). The effect of temperature on immature shore fly development has been studied to some extent by other researchers (Vänninen 2001, Fischer and Gros 2004); however, life table statistics have been estimated only at 25°C. Specific knowledge of life table statistics over a range of temperatures is essential to understanding shore fly population dynamics and may aid in assessing and exploiting the potential of biological control agents through com-

parison of the fecundity of the pest in the presence and absence of natural enemies (Bellows et al. 1992). The effects of temperature on development (checked at 24-h intervals) have been studied using shore fly populations and algal species collected only from European greenhouses; we felt it would be useful to have more refined development and life table information from North American species for comparison (checked at 12-h intervals). Because most research on biological control of shore flies has been conducted in Europe, this information could enhance our ability to conduct biological assessments of natural enemies native to North America if differences among the shore fly development times are found. Therefore, experiments were undertaken to determine the effects of temperature on development, longevity, and reproduction of shore flies.

An additional objective of this study was to develop a rearing method that could be used in biological assessments of shore fly natural enemies and would simplify the daily monitoring process and enable rapid identification of life stages while supporting high rates of survival (low natural mortality).

Materials and Methods

Source, Maintenance, and Use of Algae. A mixed algal community including at least two species of green algae (Chlorophyceae: Chlorococcales) in the family Scenedesmaceae and an unidentified coccoid cyanobacterium (blue green alga) were prepared by

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mixing a small amount of water supporting algal growth obtained from a research greenhouse located at Cornell University and adding it to a 10-liter plastic bucket that was filled with water containing a low concentration of fertilizer (200 ppm, Excel 21–5-20 (N-P-K); Scotts-Sierra Horticultural Products, Marys-ville, OH). To prepare algae-infested filter paper for use in biological assays, rockwool slabs (Grodan AO cubes; Agro Dynamics, Coppell, TX), measuring 51 by 25 cm, were placed in plastic trays that lacked drainage holes. The flats containing rockwool were filled such that the surface of the rockwool was submerged under 1–2 mm of the algae-inoculated water/fertilizer solu-tion. Flats were covered with transparent plastic domes to prevent infestation by any shore flies po-tentially present in the greenhouse. The algae-rock-wool trays were incubated in a glass greenhouse at 24 ± 6°C, under a natural light regimen of ≈14:10 h light/dark. All subsequent algal cultures were pre-pared using the algal stock contained in the original bucket, which was refilled with dilute fertilizer solution after each use. The algae-rockwool trays were allowed to incubate for a minimum of 4 d. Filter paper disks of desired sizes were placed onto the surface of the rockwool, and the dome was replaced. The disks were rapidly colonized by algae and were incubated 2–5 d before use. Fertilizer solution was added to the algae-rockwool trays as needed to keep the filter paper slightly submerged and ensure profuse algal growth.

Temperature-Dependent Development of Imma-ture Shore Flies. Eggs for use in larval development assays were obtained by placing 30–40 adult shore flies onto an algae-infested filter paper disk (90 mm diameter) in a petri dish that was covered with its lid and sealed with Parafilm "M" (Pechiney Plastic Pack-aging, Chicago, IL). Adult shore flies were collected from research greenhouses located at Cornell Univer-sity, Ithaca, NY, in February–March, 2006, by mouth aspiration into 20-ml scintillation vials, cold-anesthe-tized for 3–4 min at 7°C, and placed into the ovipo-sition dishes. Oviposition dishes were randomly di-vided into three groups (two or three replicate dishes per group) and placed into each of three environ-mental incubators (Percival, Boone, IA) with nominal settings of 20, 25, or 28°C (16:8 h L:D). Temperature was recorded hourly in each incubator using a Hobo electronic data logger (Onset Computer, Bourne, MA). The oviposition dishes in each incubator were incubated for 4 h, and the adult shore flies were re-moved. Forty eggs per temperature regimen were arbitrarily selected from the dishes and placed indi-vidually onto 2.5-cm-diameter algae-colonized filter papers in 35-mm-diameter petri dishes. The filter pa-pers used in these dishes were taken from a single rockwool-culture tray and placed directly into the petri dishes without addition of extra water. The petri dishes were covered with stretched parafilm rather than lids to prevent escape of larvae. Thirty-five mi-croliters of the previously described dilute fertilizer solution was added to each dish every 1–3 d as needed until larval pupation; care was taken to avoid pooling. Thereafter, no additional water was added. Petri dishes with shore fly eggs, larvae, and pupae were checked every 12 h until adult emergence. Egg hatch, larval molting, pupation, and adult emergence was determined by the presence of a first-instar larva, the presence of one or two pairs of mouth hooks (second and third instars, respectively), a puparium, and an adult shore fly, respectively. The experiment was con-ducted twice (test 1 and test 2), with the tests being separated by an interval of 4 wk. The second test used 30 eggs per temperature. Additionally, temperature regimens were rerandomized among incubators after the first test.

Female Fecundity, Oviposition Period, and Adult Longevity. At the end of each of the larval development studies (tests 1 and 2), 10 newly emerged adult female shore flies (≤36 h old) were randomly selected from each of the three temperatures, paired with males from the same respective temperature regimen, and placed into 35-mm petri dishes (one pair/dish) provisioned with a 2.5-cm-diameter algae-infested filter paper disk. A total of 60 pairs of flies were selected (10 pairs/temper-ature/test). Petri dishes were covered with their lids, sealed with parafilm, and incubated at the temperature at which they developed. Each pair was transferred ev-ery 24 h to a new petri dish with a fresh algal disk until both male and female shore flies died. The total number of eggs laid each day was recorded, as was the day of death for both the male and female shore flies. These data were used to record preoviposition and oviposition pe-riods for each female. If a female outlived its paired male, the male was replaced with a greenhouse-collected male of unknown age.

Statistical Analysis. All analyses were conducted us-ing the software package JMP version 5 (SAS Institute 2002). Analyses of variance (ANOVAs) studying effects of temperature on each immature life stage were con-ducted using data from all insects that completed that life stage. Sex was not determined for insects that died pre-maturely, and therefore, ANOVAs that included sex as a main effect included only those insects that completed development to adulthood. Development times were expressed in units of days. Because time event response data, e.g., times for completion of a life stage or times until death, are generally not normally distributed, each anal-ysis was confirmed by an additional ANOVA after rank transformation of the data, a procedure equivalent to the nonparametric Kruskal-Wallis test (Conover 1999). Nonparametric tests of interaction were conducted and evaluated as recommended by Conover (1999). Results regarding significance of main effects and interactions from ANOVA of the rank-transformed data were com-pared with those from parametric ANOVA of $\log(x + 1)$-transformed data. If results from the two analyses were similar, the findings of the parametric ANOVA were accepted.

Median survival times (ST_{50}) and 95% confidence intervals for male and female shore flies were esti-mated by application of the nonparametric Turnbull method, which accounts for interval-censored data (SAS Institute 2002), followed by parametric linear modeling. Turnbull survival curves were examined for fit to the log normal versus Weibull distributions, and

Table 1. Mean development times (±SE) of *S. tenuicosta* life stages fed algae and incubated at constant 20, 26, or 28.5°C

Temperature	Sex	N	Development time (in days)						
			Egg	First instar	Second instar	Third instar	Combined larval instars	Pupae	Egg to adult
20°C[a]	Female	35	1.70 ± 0.04	1.70 ± 0.04	1.76 ± 0.05	3.34 ± 0.23	6.80 ± 0.23	5.87 ± 0.06	14.37 ± 0.27
	Male	29	1.74 ± 0.05	1.78 ± 0.05	1.64 ± 0.04	3.17 ± 0.11	6.59 ± 0.12	6.29 ± 0.08	14.62 ± 0.20
	Mean		1.72 ± 0.02	1.74 ± 0.04	1.70 ± 0.06	3.26 ± 0.09	6.70 ± 0.11	6.08 ± 0.21	14.50 ± 0.13
Fischer and Gros, 20°C[b]		30	2.1 ± 0.32	1.0 ± 0.00	2.0 ± 0.19	1.0 ± 0.56	4.4 ± 0.57	6.7 ± 0.45	13.2 ± 0.57
Vïnninen, 20°C[c]		133	2.4 ± 0.03	—	—	—	7.4 ± 0.08	6.2 ± 0.07	15.9 ± 0.08
26°C[a]	Female	26	1.00 ± 0.00	1.00 ± 0.00	1.02 ± 0.02	1.73 ± 0.05	3.75 ± 0.05	3.37 ± 0.08	8.12 ± 0.09
	Male	39	1.00 ± 0.00	1.00 ± 0.00	0.99 ± 0.01	1.78 ± 0.04	3.77 ± 0.04	3.44 ± 0.07	8.21 ± 0.07
	Mean		1.00 ± 0.00	1.00 ± 0.00	1.01 ± 0.02	1.76 ± 0.03	3.76 ± 0.01	3.41 ± 0.04	8.17 ± 0.05
Fischer and Gros, 25°C[b]		20	1.8 ± 0.06	1.0 ± 0.00	1.0 ± 0.23	1.4 ± 0.50	3.4 ± 0.51	3.7 ± 0.48	9.1 ± 0.25
Vïnninen, 25°C[c]		99	1.1 ± 0.08	—	—	—	6.0 ± 0.12	4.5 ± 0.07	11.4 ± 0.14
28.5°C[a]	Female	31	0.81 ± 0.04	0.81 ± 0.04	0.84 ± 0.04	1.47 ± 0.04	3.11 ± 0.04	3.08 ± 0.06	7.00 ± 0.07
	Male	29	0.71 ± 0.05	0.84 ± 0.04	0.95 ± 0.04	1.40 ± 0.05	3.19 ± 0.06	3.17 ± 0.04	7.07 ± 0.07
	Mean		0.76 ± 0.05	0.83 ± 0.02	0.90 ± 0.06	1.44 ± 0.04	3.15 ± 0.04	3.13 ± 0.05	7.04 ± 0.04

[a] Development times (days) of shore flies reared on algae-infested filter paper at constant 20, 26, or 28.5°C; flies monitored at 12-h intervals.
[b] Development times (days) of shore flies reared on algae-infested water agar at constant 20 or 25°C; flies monitored at 24-h intervals; data from Fischer and Gros (2004).
[c] Development times (days) of shore flies reared on algae-infested rockwool kept at constant 20 or 25°C; flies monitored at 24-h intervals; data from Vnninen (2001).

the Weibull model was selected as providing the best fit for ST_{50} estimations.

Development times for each life stage, as well as the total larval and total development time from egg to adult, were used to calculate development rates (1/ development time), which were regressed against temperature. The regression parameters and slopes were used to estimate the lower temperature threshold for development (t) and the thermal constant K, as described by Campbell et al. (1974).

Survivorship data for each life stage, expressed as days alive, was used to calculate stage-specific life tables for each of the three temperatures. The effect of temperature on the proportion of each cohort surviving to adulthood was tested by χ^2 analysis. Daily survivorship and age-specific fecundity of adult females were used to estimate the intrinsic rate of natural increase (r_m) for shore flies reared at each of the three temperatures using the following formula: $\sum (e^{-rx})l_x m_x = 1$, where x = age of adult flies, l_x = proportion surviving on day x, and m_x = female eggs/ female on day x. The number of female eggs/female laid on day x was calculated by dividing the total eggs/d by two. The sex ratio of the adults that emerged in the development study (see Results) as well as data from Vänninen (2001) suggested a 1:1 sex ratio. The net reproductive rate (R_0) for each temperature was calculated using the equation $R_0 = \sum l_x m_x$; generation time (T) and doubling time (DT) for each temperature were calculated using equations $T = \ln R_0/r$ and $DT = \ln 2/r$, respectively, as per Birch (1948).

Results

Comparison of Data from Replicate Tests. The mean (range) of temperatures recorded in the environmental incubators set to 20, 25, and 28°C were 20.5 (19.8–21.0), 26.5 (25.2–27.9), and 28.2°C (28.1–28.7°C) in test 1 and 19.7 (18.7–20.2), 25.8 (25.1–26.7), and 28.7°C (27.3–29.5°C) in test 2, respectively. Hereafter, the actual temperatures will be referred to as 20, 26, and 28.5°C. When temperature was included in the model as a categorical variable designated as 20, 26, or 28.5°C, the times for immature development (egg to adult) at the three temperatures differed significantly between the two replicate tests ($F_{(1,177)} = 60.4$; $P < 0.0001$), and there was a test × temperature interaction ($F_{(2,177)} = 8.0$; $P = 0.0005$). When temperature was included in the model as a continuous variable and the actual temperatures recorded for each test were used, there was an effect of test on immature development ($F_{(1,181)} = 12.5$, $P = 0.0005$) but no significant test × temperature interaction ($F_{(1,181)} = 0.78$; $P = 0.38$). The significant effect of test and the test × temperature interaction when temperature was described as a categorical variable are likely a result of the slight differences in temperatures (20.5 versus 19.7; 26.5 versus 25.8; 28.2 versus 28.7°C) between the two replicate tests. This is supported by the result of no significant test × temperature interaction when actual temperature was included in the model as a continuous variable. Development of the different sexes across the three temperatures was not affected by test, i.e., there was not a significant test × sex interaction ($F_{(1,177)} = 0.41$, $P = 0.52$). Similarly, male and female adult longevity and total egg production across temperatures were equivalent in the two tests ($F_{(1,52)} = 0.40$, $P = 0.53$; $F_{(1,53)} = 2.5$, $P = 0.12$; and $F_{(1,53)} = 0.19$, $P = 0.67$, respectively), with no significant test × temperature interactions ($F_{(2,52)} = 2.6$, $P = 0.08$; $F_{(2,53)} = 0.73$, $P = 0.49$; and $F_{(2,53)} = 0.16$, $P = 0.85$, respectively). In each of the above cases, ANOVA of the rank-transformed data produced results similar to the parametric ANOVA. In view of these findings, and considering that sample sizes were not markedly different between tests ($n = 40$ versus

Table 2. ANOVA *F*-test statistics for experiments studying differences caused by temperature and sex on development times of shore fly life stages maintained at constant 20, 26, and 28.5°C

Life stage	ANOVA			ANOVA of RANKS		
	Main effect of temperature[a]	Main effect of sex[b]	Temperature × sex interaction[a]	Main effect of temperature[a]	Main effect of sex[b]	Temperature × sex interaction[a]
Egg	$F = 342, P < 0.0001$	$F = 0.98, P = 0.32$	$F = 2.4, P = 0.10$	$F = 492, P < 0.0001$	$F = 1.2, P = 0.27$	$F = 2.5, P = 0.08$
First instar	$F = 277, P < 0.0001$	$F = 1.2, P = 0.28$	$F = 0.3, P = 0.74$	$F = 459, P < 0.0001$	$F = 0.86, P = 0.36$	$F = 0.23, P = 0.79$
Second instar	$F = 244, P < 0.0001$	$F = 0.04, P = 0.84$	$F = 5.1, P = 0.007$	$F = 467, P < 0.0001$	$F = 0.09, P = 0.77$	$F = 5.2, P = 0.006$
Third instar	$F = 297, P < 0.0001$	$F = 0.31, P = 0.58$	$F = 0.68, P = 0.51$	$F = 368, P < 0.0001$	$F = 0.01, P = 0.91$	$F = 0.99, P = 0.37$
Combined larval instars	$F = 948, P < 0.0001$	$F = 0.001, P = 0.97$	$F = 0.84, P = 0.44$	$F = 565, P < 0.0001$	$F = 0.82, P = 0.37$	$F = 0.73, P = 0.49$
Pupa	$F = 934, P < 0.0001$	$F = 8.6, P = 0.004$	$F = 1.3, P = 0.28$	$F = 276, P < 0.0001$	$F = 6.8, P = 0.01$	$F = 0.77, P = 0.46$
Egg to adult	$F = 2082, P < 0.0001$	$F = 2.0, P = 0.16$	$F = 0.12, P = 0.88$	$F = 682, P < 0.0001$	$F = 4.5, P = 0.04$	$F = 0.71, P = 0.49$

[a] *F*-tests with 2,183 degrees of freedom.
[b] *F*-tests with 1,183 degrees of freedom.

30), it was decided that the pooled data would adequately predict response at the mean temperatures of 20, 26, and 28.5°C. Data from the two tests were therefore pooled for all analyses reported in the subsequent sections.

Temperature-Dependent Development of Immature Shore Flies. Increasing temperature significantly reduced the duration of the egg stage, the first, second, and third larval stadia, as well as the pupal stadium. Additionally, there was no significant difference between male versus female development times for any shore fly life stage with the exception of the pupal stage (Tables 1 and 2). Egg-to-adult development was completed in 14.5, 8.2, and 7.0 d at 20, 26, and 28.5°C, respectively (Table 1), and of the 189 larvae that emerged as adults, 92 were female and 97 were male, yielding an ~1:1 sex ratio.

The regression of development rate of each life stage on temperature and extrapolation to the zero development rate estimated low-temperature development thresholds of ≈12–14°C, and the threshold for development from egg to adult was estimated at 12.1°C (Table 3). This value is markedly higher than the estimates of 6.4°C of Vänninen (2001) and 8.2°C of Fischer and Gros (2004). Fischer and Gros (2004) tested a low temperature of 12°C, whereas the lowest temperature tested in this study and the study of Vänninen (2001) was 20°C. Because the study of Fischer and Gros (2004) represents a substantially lesser degree of extrapolation, this value may be assumed the most accurate and strongly suggests that our estimate of 12.1°C is an overestimate (likely because of extrap-

olation error). Accepting the value of Fischer and Gros (2004) as the best available estimate of the low-temperature threshold, these data indicate that 154.4 ± 1.2 thermal units (degree days) are needed for development from egg to adult. Thermal unit requirements for each life stage are presented in Table 3.

Developmental stage-specific mortality (dx, percent mortality with respect to the total number of individuals entering a stadium) was relatively low at all temperatures for all life stages, with maximum percent mortalities of 5.7% occurring in both the egg stage and in the third instar (Table 4). No mortality was observed during the first or second instars at any of the three temperatures tested. With regard to the total percent mortality over the course of shore fly development (total number of insects dying with respect to the total number of insects in the original cohort), there were no significant differences among the three temperatures ($\chi^2_{(2)} = 2.1, P = 0.34$).

Female Fecundity, Oviposition Period, and Adult Longevity. There was a significant effect of temperature on the preoviposition period of adult female shore flies ($F_{(2,52)} = 10.1, P = 0.0002$). The preoviposition period at 28.5°C was significantly shorter than the preoviposition periods at 20 and 26°C, which did not differ significantly from each other (Table 5). The mean oviposition period, the number of days from the first to last day of oviposition, was longer at 26°C (15.0 ± 2.2 d) than at 20 or 28.5°C (14.3 ± 2.1 and 10.8 ± 1.4 d, respectively); however, the differences were not statistically significant ($F_{(2,56)} = 0.7, P = 0.50$). Similarly, lifetime fecundity of shore flies reared

Table 3. Linear regression parameters incorporating development rate as the dependent variable and temperature as the independent variable, low-temperature threshold for development (t), and thermal constant (K) for each life stage of *S. tenuicosta*

Life stage	Intercept ± SE	Slope ± SE	R^2	P value	t ± SE (°C)	K ± SE[a]	K ± SE[b]
Egg	-1.351 ± 0.133	0.094 ± 0.005	0.703	<0.0001	14.4 ± 2.0	10.6 ± 0.5	18.0 ± 0.3
First instar	-1.201 ± 0.134	0.088 ± 0.005	0.625	<0.0001	13.6 ± 1.6	11.4 ± 0.6	18.5 ± 0.3
Second instar	-0.901 ± 0.136	0.074 ± 0.005	0.506	<0.0001	12.1 ± 1.2	13.5 ± 0.8	19.0 ± 0.3
Third instar	-0.620 ± 0.054	0.046 ± 0.002	0.726	<0.0001	13.5 ± 0.6	21.7 ± 0.9	33.5 ± 0.7
Combined larval instars	-0.254 ± 0.011	0.020 ± 0.0004	0.922	<0.0001	12.7 ± 0.2	50.0 ± 1.0	70.8 ± 0.8
Pupa	-0.232 ± 0.015	0.020 ± 0.001	0.864	<0.0001	11.6 ± 0.1	50.0 ± 2.5	65.7 ± 0.6
Egg to adult	-0.109 ± 0.003	0.009 ± 0.0001	0.968	<0.0001	12.1 ± 0.1	111.1 ± 1.2	154.4 ± 1.2

[a] Thermal constant ± SE based on t values (tabulated) from this study.
[b] Thermal constant ± SE based on t value of 8.2°C estimated by Fischer and Gros (2004).

Table 4. Life table of *S. tenuicosta* reared at constant 20, 26, and 28.5°C

Temperature	Stage	a_x (number observed at start of each stage)	l_x (proportion surviving to start of each stage)	Number dying in each stage	d_x (proportion of original cohort dying during each stage)	q_x (mortality rate; stage specific)
20°C	Egg	70	1.0000	1	0.0143	0.0143
	First instar	69	0.9857	0	0.0000	0.0000
	Second instar	69	0.9857	0	0.0000	0.0000
	Third instar	69	0.9857	4	0.0571	0.0580
	Pupa	65	0.9286	1	0.0143	0.0154
	Adult	64	0.9143			
26°C	Egg	70	1.0000	4	0.0571	0.0571
	First instar	66	0.9429	0	0.0000	0.0000
	Second instar	66	0.9429	0	0.0000	0.0000
	Third instar	66	0.9429	0	0.0000	0.0000
	Pupa	66	0.9429	1	0.0143	0.0152
	Adult	65	0.9286			
28.5°C	Egg	70	1.0000	3	0.0429	0.0429
	First instar	67	0.9571	0	0.0000	0.0000
	Second instar	67	0.9571	0	0.0000	0.0000
	Third instar	67	0.9571	4	0.0571	0.0597
	Pupa	63	0.9000	3	0.0429	0.0476
	Adult	60	0.8571			

at 26°C (709.8 ± 119.4 eggs/female) was 1.9 and 1.5 times greater than fecundity of females incubated at 20 and 28.5°C, respectively, but the differences were not significant ($F_{(2,56)}$ = 2.0, P = 0.15; Table 5). Average daily lifetime egg production varied significantly as a function of temperature ($F_{(2,56)}$ = 4.5, P = 0.02), with insects incubated at 26°C laying 2.1 and 1.1 times more eggs each day compared with insects incubated at 20 and 28.5°C, respectively (Table 5).

Daily offspring production per surviving female shore fly (referred to as the age-specific rate of offspring production) was plotted for each temperature (Fig. 1). It is important to note that these means are based on decreasing numbers of females over time. As expected, the data revealed a reduction in offspring production with increasing age of the shore flies. The response pattern was anomalous at 28.5°C because of the exceptional longevity and fecundity of a single individual. Maximum rates of oviposition were otherwise recorded within the first 7–10 d after emergence. Cohort-specific rates of reproduction are based on the total number of females used to initiate the two tests and thus reflect the time-dependent decrease in offspring production by the treatment cohort as a whole, caused by both increasing age and mortality of the individuals comprising the cohort (each mean incorporating zero values for deceased individuals). These rates are presented in Fig. 2. Maximum oviposition by

the cohorts at 20, 26, and 28.5°C occurred on days 9, 6, and 5, respectively.

ANOVA indicated that adult male longevity was significantly affected by temperature ($F_{(2,55)}$ = 4.9, P = 0.01). Males maintained at 26°C lived 24.8 ± 1.9 d, which was 1.3 and 1.7 times longer than males maintained at 20 and 28.5°C, respectively (Table 5). It was not possible to detect a significant effect of temperature on mean survival of females using ANOVA ($F_{(2,56)}$ = 2.4, P = 0.10); however, a significant effect was found by comparing the Turnbull survivorship curves fit to the Weibull distribution (Table 6). ST_{50}s of females reared at 20 and 26°C were 49 and 40% longer, respectively, than shore flies reared at 28.5°C (Table 6). Examination of the survivorship data for the immature (Table 4) and adult shore flies (Fig. 1) revealed that, at each of the tested temperatures, mortality acted most heavily against old individuals. This corresponds to a type I mortality distribution (see Southwood 1978 and Begon et al. 1990).

The life table statistics of adult female shore flies are presented in Table 7. The highest net reproductive rate (R_o) was obtained for insects reared at 26°C, followed by insects reared at 28.5 and 20°C (329.6, 204.3, and 183.9, respectively). The intrinsic rate of natural increase (r_m) was highest at 28.5°C and was followed by insects incubated at 26 and 20°C (0.430, 0.396, and 0.217, respectively). Generation time (G)

Table 5. Mean (±SE)[a] oviposition period, total and daily fecundity, and male and female longevity, in days, of shore flies reared at constant 20, 26, and 28.5°C

Temperature	Preoviposition period	Oviposition period	Total fecundity[b]	Daily fecundity[c]	Male longevity	Female longevity
20°C	2.8 ± 0.3 a	14.3 ± 2.1 a	378.8 ± 61.5 a	16.3 ± 2.3 a	18.6 ± 2.4 ab	21.8 ± 2.2 a
26°C	2.3 ± 0.1 a	15.0 ± 2.2 a	709.8 ± 119.4 a	33.5 ± 3.8 b	24.8 ± 1.9 a	19.9 ± 2.4 a
28.5°C	1.7 ± 0.2 b	10.8 ± 1.4 a	476.8 ± 83.0 a	29.7 ± 3.5 a	14.8 ± 1.9 b	15.0 ± 1.4 a

[a] Means followed by same letter are not significantly different based on the Tukey HSD test (α = 0.05).
[b] Shore flies reared on algae-colonized filter paper in parafilm-sealed petri dishes.
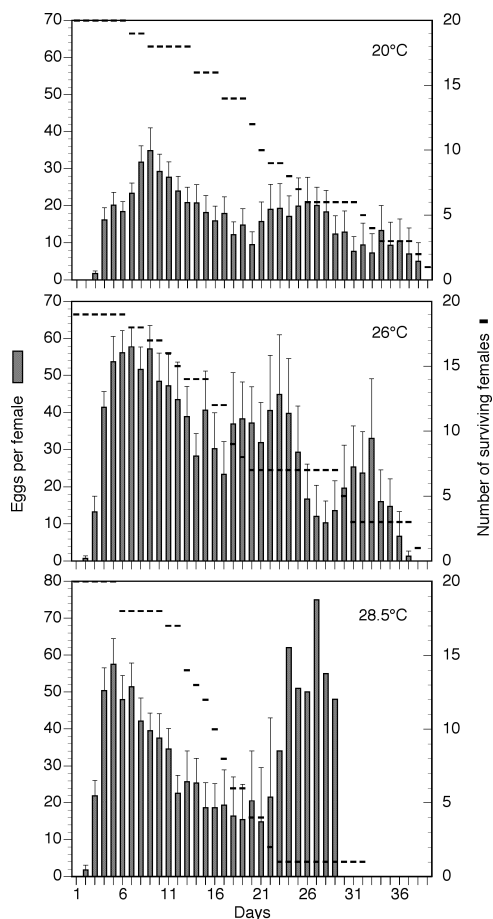[c] Daily lifetime fecundity (calculated for each female as total eggs produced divided by age at death).

Fig. 1. Age-specific mean daily rate of egg production and survivorship of adult female shore flies provided fresh algae daily and maintained at constant 20, 26, or 28.5°C. Error bars indicate SE.
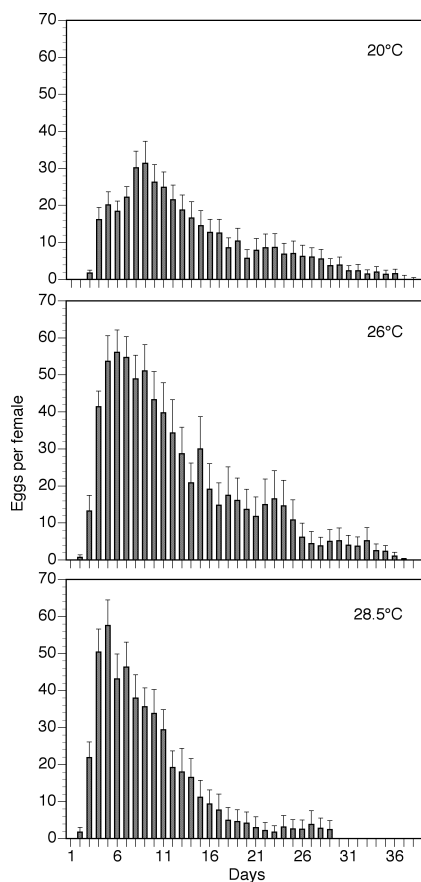

Fig. 2. Cohort-specific mean daily rate of egg production of adult female shore flies provided fresh algae daily and maintained at constant 20, 26, or 28.5°C. Error bars indicate SE.

was 24.0, 14.6, and 12.4 d at 20, 26, and 28.5°C, respectively, and doubling time of the population at these three temperatures was 3.2, 1.8, and 1.6 d, respectively.

Discussion

As expected, the duration of each immature stadium and thus the total development time from egg to adult decreased as temperature increased from 20 to 28.5°C (Table 1). Interestingly, for each of the three temperatures, the duration of the egg stage and the first and second stadia were approximately equal, but the third stadium was twice as long as any preceding stage. Total duration of the three larval stadia combined was approximately equal to the duration of the pupal stadium at each of the three temperatures (Table 1).

The range of temperatures used in this study was roughly the same as that used by Vänninen (2001) and within the range of temperatures used by Fischer and Gros (2004). Two temperatures, constant 20 and ≈25°C, were used in all three studies. It is noted that, despite the use of the name *Scatella stagnalis* Fallen in

Vänninen (2001), the species was in fact *S. tenuicosta* Collin, as stated in Vänninen and Koskula (2003). This clarification, as well as the similar temperatures of 20 and 25–26°C, allows for general comparisons of results generated among these three studies.

Vänninen (2001) did not determine the duration of each larval stadium, but reported average development times for the egg, combined larval stages, pupa, and egg to adult. Fischer and Gros (2004) did determine the average duration of all shore fly life stages. Among the three studies, the reported average dura-

Table 6. Median survival times (ST_{50}) of adult male and female shore flies reared at three temperatures

Temperature	Male ST_{50} (95% CI)[a]	Female ST_{50} (95% CI)[a]
20°C	18.1 (14.7–22.4) ab	21.1 (17.6–25.3) a
26°C	22.1 (17.9–27.3) a	19.9 (16.5–24.0) ab
28.5°C	14.5 (11.8–17.7) b	14.2 (11.8–17.0) b
	$\chi^2_{(2)} = 7.65$, $P = 0.0218$	$\chi^2_{(2)} = 10.65$, $P = 0.0133$

[a] Median survival times followed by same letter are not significantly different based on likelihood-ratio χ^2 tests with Bonferroni-adjusted α ($\alpha = 0.0167$).

Table 7. Demographical patterns[a] of algae-fed adult female *S. tenuicosta*, incubated at constant 20, 26, and 28.5°C

20°C				26°C				28.5°C			
x	n_x	l_x	m_x	x	n_x	l_x	m_x	x	n_x	l_x	m_x
1		1.000	0.000	1		1.000	0.000	1		1.000	0.000
15	20	0.914	0.000	8	19	0.929	0.000	7	20	0.857	0.000
16	20	0.914	0.875	9	19	0.929	0.342	8	20	0.857	0.850
17	20	0.914	8.075	10	19	0.929	6.605	9	20	0.857	10.925
18	20	0.914	10.075	11	19	0.929	20.711	10	20	0.857	25.175
19	20	0.914	9.200	12	19	0.929	26.816	11	20	0.857	28.775
20	20	0.914	11.684	13	19	0.929	28.053	12	18	0.771	23.972
21	19	0.869	15.868	14	18	0.880	28.861	13	18	0.771	25.722
22	19	0.869	17.417	15	18	0.880	25.806	14	18	0.771	21.056
23	18	0.823	14.611	16	17	0.831	28.559	15	18	0.771	19.778
24	18	0.823	13.806	17	17	0.831	24.176	16	18	0.771	18.750
25	18	0.823	11.972	18	16	0.782	23.594	17	17	0.729	17.265
26	18	0.823	10.417	19	15	0.733	21.733	18	17	0.729	11.265
27	18	0.823	10.375	20	14	0.684	19.464	19	14	0.600	12.857
28	16	0.731	9.063	21	14	0.684	14.143	20	13	0.557	12.692
29	16	0.731	7.938	22	14	0.684	20.321	21	12	0.514	9.292
30	16	0.731	8.929	23	12	0.586	15.125	22	10	0.429	9.300
31	14	0.640	6.107	24	12	0.586	11.667	23	8	0.343	9.625
32	14	0.640	7.393	25	9	0.440	18.444	24	6	0.257	8.167
33	14	0.640	4.750	26	8	0.391	19.125	25	6	0.257	7.667
34	12	0.549	7.850	27	7	0.342	18.571	26	4	0.171	10.250
35	10	0.457	9.500	28	7	0.342	15.929	27	4	0.171	7.375
36	9	0.411	9.611	29	7	0.342	20.286	28	2	0.086	10.750
37	9	0.411	8.563	30	7	0.342	22.429	29	1	0.043	17.000
38	8	0.366	9.929	31	7	0.342	19.857	30	1	0.043	31.000
39	7	0.320	10.417	32	7	0.342	14.643	31	1	0.043	25.500
40	6	0.274	10.000	33	7	0.342	8.357	32	1	0.043	25.000
41	6	0.274	9.167	34	7	0.342	6.000	33	1	0.043	37.500
42	6	0.274	6.167	35	7	0.342	5.143	34	1	0.043	27.500
43	6	0.274	6.417	36	7	0.342	6.786	35	1	0.043	24.000
44	6	0.274	3.833	37	5	0.244	9.800	36	1	0.043	0.000
45	6	0.274	4.700	38	3	0.147	12.667	37	1	0.043	0.000
46	5	0.229	3.625	39	3	0.147	11.833	38	1	0.043	0.000
47	4	0.183	6.667	40	3	0.147	16.500				
48	3	0.137	4.667	41	3	0.147	8.000				
49	3	0.137	5.167	42	3	0.147	7.333				
50	3	0.137	0.000	43	3	0.147	3.333				
51	3	0.137	0.000	44	3	0.147	0.667				
52	2	0.091	0.000	45	1	0.049	0.000				
53	1	0.046	0.000								

[a] x = age of adult females (days); n_x = no. of adult females on day x; l_x = proportion of females surviving on day x; m_x = female eggs per female on day x.

tion of the egg stage never differed by >1 d, ranging from 1.7 to 2.4 d at 20°C and 1.0–1.8 d at 25–26°C (Table 1). Comparing this study and the study of Fischer and Gros (2004), only the duration of the third stadium at 20°C differed by >1 d. Fischer and Gros (2004) reported the average duration of the third stadium to be 1.3 d at 20°C, which, surprisingly, is less than one third the time we observed (3.3 d, Table 1). Average duration of all larval stadia combined was longest in Vänninen (2001) and ranged from 4.4 to 7.4 d at 20°C and from 3.4 to 6.0 d at 25–26°C, across the three studies. Development time from egg to adult was longest at both temperatures in Vänninen (2001) and differed by ~1 d between this study and that of Fischer and Gros (2004) for either temperature (Table 1).

The average total fecundities of adult female shore flies in this study, although not statistically different, varied greatly among the temperatures tested. The average total number of eggs laid was greatest at 26°C, intermediate at 28.5°C, and lowest at 20°C. The same

pattern occurred for the daily rate of egg production, and the effect of temperature was statistically significant. This suggests that 26°C is near optimum for reproduction; however, the shore flies developed fastest at 28.5°C, and thus the highest value for the intrinsic rate of natural increase (r_m) was greatest at 28.5°C. Additionally, as temperature increased from 20 to 28.5°C, generation time (T) and population doubling time (DT) decreased by approximately one half. These results indicate that this *S. tenuicosta* population is more fit at 28.5°C than at 20 or 26°C.

Adult fecundity and longevity were measured at three temperatures in this study and at only a single temperature in Vänninen (2001) (25°C) and Fischer and Gros (2004) (20°C). Comparing the results herein with those of Fischer and Gros (2004) at 20°C, Fischer and Gros reported a similar preoviposition period lasting ≈3 d, a longer oviposition period (2 d longer), twice the number of eggs per day per female, 1.4 times greater total fecundity, and greater longevity of adults (both male and female shore flies lived nearly 2 d

longer than the shore flies in this study). However, the shore flies in this study were apparently more fit than those used by Vänninen (2001), with the females exhibiting, at 25–26°C, a shorter preoviposition period (2.3 versus 3.2 d), greater daily fecundity (34 versus 20 eggs/d), greater total fecundity (710 versus 316 eggs), and greater longevity (19.9 versus 15.5 d). Moreover, the net reproductive rate of the insects in this study was 2.5 times greater, the intrinsic rate of natural increase was higher, and both the generation time and doubling time were shorter compared with the values reported by Vänninen (2001). Fischer and Gros (2004) did not report life table parameters.

The differences in the values for development times and life table parameters of the insects among these three studies could, in some cases, be a result of differences in experimental methods. In the studies investigating developmental times of immature shore flies, the time interval at which larval insects were checked for molting differed substantially. Both Fischer and Gros (2004) and Vänninen (2001) checked their insects every 24 h, whereas insects in this study were checked every 12 h. The substantially shorter time interval between checks would be expected to yield more accurate estimates of developmental times for each life stage. The bioassay system used also differed for all three studies. Our studies were conducted in petri dishes with filter paper supporting algal growth, whereas Vänninen (2001) conducted studies in cell plates on rockwool supporting algal growth, and Fischer and Gros (2004) used petri dishes with agar supporting algae. The algal species complexes commonly found in greenhouses located in the different geographic regions in which the studies were conducted, the northeastern United States and Europe, may have been different. The algae used by Fischer and Gros (2004), Vänninen (2001), and in this study belonged to the Chlorophyceae and Cyanophyceae, although none of the studies identified the algae to the species level or determined the relative biomasses of the different taxa. The algal species serving as the principal food source is known to affect developmental times and adult longevity and fecundity (Foote 1995 and references therein). It is also possible that the resident populations of *S. tenuicosta* in these regions have developed slight biological difference as a result of unknown environmental selection pressures. Without direct comparisons of the insects from each region in a standardized bioassay system, using a standardized algal diet, the differences cannot be readily explained.

This study adds to Vänninen (2001) and Fischer and Gros (2004), by providing more accurate estimates of stage-specific immature developmental duration based on checks made at 12-h intervals. This paper also provides new information on life table statistics and demographic patterns of *S. tenuicosta* at several temperatures that commonly occur in greenhouses. These results can be used to predict the time needed to achieve a given larval instar at a specific temperature and will aid in the planning of experiments that need the use of specific shore fly instars. Comparing estimates of r_m for natural enemy species with that for

shore flies and comparing shore fly r_m values in the presence and absence of natural enemies can also be useful in assessing biological control potential and developing biologically based integrated pest management (IPM) systems (Van Driesche et al. 1994).

To conduct the experiments aimed at determining the duration of immature shore fly instars and life table parameters, a novel shore fly egg collection technique and rearing system were developed that entailed the use of algae-infested filter paper contained in parafilm-sealed petri dishes. The described rearing system provided for easy collection of large numbers of eggs, direct observations for determination of life stage, rapid assessment of the condition of test subjects (e.g., alive versus dead), and low rates of natural (control) mortality. Mortality during immature development was low at all temperatures: 8, 7, and 14% at 20, 26, and 28.5°C, respectively. This included egg mortality (defined as failure to hatch), which accounted for 38% of all developmental mortality (our estimates of egg mortality did not differentiate between unfertilized eggs laid by newly emerged unmated females and fertilized eggs that died during development and hatching). These rearing methods can be modified for a broad range of studies, e.g., biological assessment (bioassay) of shore fly natural enemies, by increasing both the size of the petri dishes and filter papers such that a larger number of individuals can be sustained (unpublished observations).

Acknowledgments

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